
SOME FLIGHT MECHANISMS OF BATS

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The flight of bats differs from that of birds in that the bats are more maneuverable. This is indicated by their skill in avoiding obstructions. However, because of their nocturnal habits, we know much less about their flight than about that of birds. The structure of their wings and the distribution and development of the flight muscles differ significantly from those of birds. Considerable work has been done on the anatomy, especially osteology and myology. I need not dwell on this except to say that one of the most important early papers in this field is that of Macalister (1873).

More knowledge is needed about the functional aspects of the structures involved. Among the contributions in this field, special attention should be paid to Vaughan (1959) who made a careful study of three species of bats in which he observed terrestrial locomotion and flight as well as their osteology and myology; Struhsaker (1961) compared the flight muscles and surface areas of flight membranes in preserved specimens.

In the present work, comparison has been made of some of the muscles as well as the membranes involved in flight. Twelve species distributed among six families have been studied. The hearts have been weighed as an indication of the ability for continuous exertion. The ventral thoracic muscles have been compared because of their accessibility and on the assumption that they are representative of the flight power although they do not include all of the flight muscles.

METHODS

Specimens were collected while roosting, shot while flying, or caught by Japanese mist nets. Soon after killing, the body weight was obtained on a torsion balance, and an outline of the spread wings, tail, and body was sketched on paper. The

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ventral thoracic flight muscles (nomenclature of Macalister, 1873), pectoralis major, pectoralis quartus, subclavius and serratus anticus were carefully dissected from one side and weighed on the torsion balance. This value doubled represented the ventral thoracic flight muscles. Likewise the heart was weighed on a Roller-Smith precision balance after the blood vessels were trimmed close to the organ, both sides being cut open to remove any remaining blood by means of filter paper.

Areas were determined from the tracings by the use of a compensating polar planimeter while the aspect ratio was calculated by dividing the wing length squared by its area. The span loading was found by dividing the weight of the

$$\text{Aspect ratio} = \frac{\text{length}}{\text{median width}} = \frac{\text{length}^2}{\text{area (length x median width)}}$$

body by the length of both wings. The glide area was calculated as the sum of the areas of both wings, the body area, and the uropatagium area. The buoyancy index was determined by the formula $\dfrac{\sqrt[2]{\text{wing area}}}{\sqrt[3]{\text{body weight}}}$. Taxonomic nomenclature is based on Hall and Kelson's (1959) Mammals of North America.

Specimens were collected along the Rio Chagres and the Rio La Jagua in Panamá during December and January of the years 1956, 1958, and 1960.

RESULTS

Heart and thoracic muscle weights are shown as per cent of body weights while the wing and glide areas are shown as square centimeters per gram of the body weight. In the tables the number of individuals in a species is shown in parentheses and the mean values and the standard errors of the means are given. Sexes are separated for body weights, otherwise the data for the two sexes are combined.

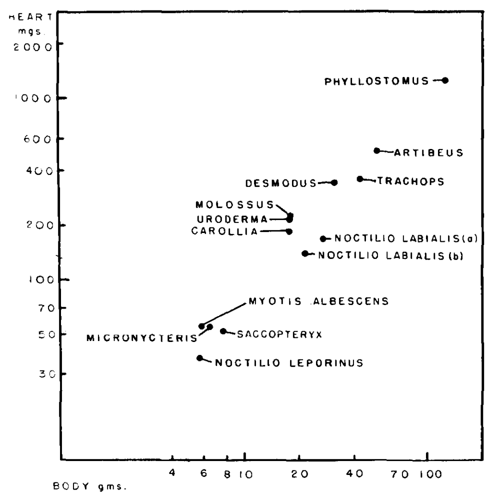

FIGURE 1. Plottings of heart weights against body weights (log scales).

Hearts

The heart weights range from 0.61 to 1.26 per cent of the body, being smallest in the Southern Bulldog Bat (*Noctilio labialis*), the Mexican Bulldog Bat (*Noctilio leporinus*), and the Greater Whitelined Bat (*Saccopteryx bilineata*) and largest in the Tentmaking Bat (*Uroderma bilobatus*), and the Bonda Mastiff Bat (*Molossus bondae*) (table 1) the others lying in the medium range. The distribution of these values is shown graphically in figure 1.

TABLE 1

Data on the locomotor mechanisms of bats

	Body Weight g	Heart % body weight	Ventral Thoracic Muscles % body weight	Wings cm²/g	Glide cm²/g	Span Loading g/cm	Aspect Ratio	Bouyancy Index
Emballonuridae								
Saccopteryx bilineata	(12♀)7.70±0.11	(12)0.68±0.02	(12)7.76±0.16	(12)12.88±0.48	(12)15.16±0.48	(12)0.29±0.01	(12)3.62±0.09	5.05
Noctilionidae								
Noctilio leporinus mexicanus	(1♀)67.50 (3♂)53.57±5.55	(3)0.65±0.07	(4)7.93±0.45	(4)5.56±0.26	(3)7.15±0.09	(4).118±0.12	(4)4.03±0.56	4.62
Noctilio labialis minor	(a)(6♀)25.78±0.63 (4♂)30.49±1.34	(10)0.61±0.01	(10)7.48±0.27	(10)5.39±0.22	(10)6.77±0.26	(10)0.57±0.01	(10)4.05±0.08	4.04
	(b)(8♀)21.39±0.04 (2♂)22.27, 24.16	(10)0.64±0.02	(10)7.68±0.16	(10)8.30±0.20	(10)9.46±0.23	(9)0.79±0.03	(9)4.10±0.04	4.81
Phyllostomidae								
Micronycteris megalotis mexicana	(3♀)6.53±0.49	(3)0.85±0.07	(3)8.63±0.87	(3)11.27±0.82	(3)13.77±0.18	(2)0.35; 0.36	2.47, 2.51	4.60
Phyllostomus hastatus	(4♀)112.8±5.6 (10♂)134.0±3.0	(14)0.96±0.03	(13)9.09±0.38	(13)3.40±0.09	(13)3.97±0.10	(13)2.34±0.06	(13)3.48±0.05	4.14
Trachops cirrhosis	(3♂)44.43±1.0 (2♂)42.80±1.10	(5)0.82±0.04	(5)9.64±0.57	(5)5.61±0.17	(5)6.41±0.35	(5)1.14±0.03	(4)2.80±0.15	4.44
Carollia perspicillata azteca	(11♀)16.99±0.53 (6♂)19.22±0.93	(17)1.03±0.02	(17)10.31±0.23	(10)8.63±0.20	(10)9.39±0.20	(10)0.58±0.02	(10)2.98±0.06	4.76
Uroderma bilobatum	(12♀)17.38±0.28 (1♂)15.65	(13)1.29±0.03	(13)11.99±0.62	(11)6.92±0.24	(11)7.82±0.18	(5)0.62±0.03	(5)3.06±0.13	4.16
Artibeus jamaicensis	(1♀)44.74 (2♂)45.42, 72.42	(3)0.93±0.09	(3)10.03±0.62	(3)4.55±0.27	(3)5.23±0.27	(3)1.49±0.18	(3)2.78±0.08	4.14
Desmodontidae								
Desmodus rotundus murinus	(3♀)33.44±2.39 (3♂)29.92±1.85	(6)1.08±0.06	(6)8.94±0.21	(6)4.88±0.26	(5)5.61±0.22	(6)1.11±0.06	(6)2.66±0.12	3.94
Vespertilionidae								
Myotis albescens	(4♀)6.16±0.36 (1♂)4.86	(5)0.94±0.04	(5)7.12±0.31	(5)11.09±0.73	(5)13.00±0.48	Lost	Lost	4.50
Molossidae								
Molossus bondae	(5)15.96–0.53 (13)18.18–0.26	(18)1.20–0.09	(18)10.86±0.30	(18)4.03±0.16	(17)5.21±0.14	(13)0.68±0.03	(12)3.68±0.09	3.29

Ventral Thoracic Muscles

The combined weights of these muscles range from 7.12 to 11.99 per cent of the weight of the body, being smallest in the Paraguay Myotis (*Myotis albescens*) and largest in the Tent-making Bat (*Uroderma bilobatus*) (table 1). Figure 2 shows the values for the different species.

The members of the two families, Emballonuridae and Noctilionidae possess hearts and ventral thoracic muscles of the same percentage of the body weight, but their wing areas differ greatly in relation to body weight. The ranges of relative heart and ventral thoracic weights vary considerably in the several species of the Phyllostomidae while the wing areas show even greater range.

The heart and ventral thoracic muscles were weighed in four young (about ¼ adult weight) of the Spear-nosed Bat (*Phyllostomus hastatus*) and in one young (about ¼ adult weight) Vampire Bat (*Desmodus rotundus*). In both species the hearts were two thirds of the percentage for adults. The ventral thoracic muscles of the young Spear-nosed Bats were one-third of the percentages for adults while in the young Vampire Bat they were only one-tenth of the percentage for adults.

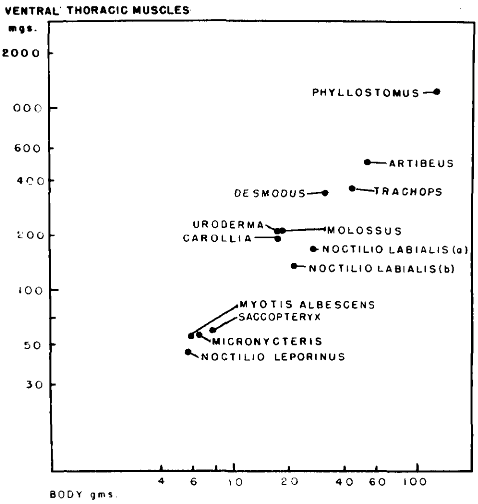

FIGURE 2. Plottings of ventral thoracic muscle weights against body weights (log scales).

Flight and Glide Areas

The range in wing areas is from 12.88 to 3.40 cm^2/g of body (table 1). Figure 3 shows the various values. Note that the relative wing areas are greater in group "b" than in group "a" of the Southern Bulldog Bat (*Noctilio labialis*). The body weights of "a" are larger than those of "b". Both groups were collected in the same area but in different years.

Glide areas range from 3.97 to 15.16 cm^2/g. These are shown in table 1 and figure 3. When one considers the definition of glide area, i.e., areas of both wings plus the body and uropatagium areas, it is obvious that wing area is the dominant factor in that of glide.

The span loading ranges from 0.29 in *Saccopteryx* sp. to 2.34 in *Phyllostomus* sp. and is quite variable among the different species. The larger bats show the greater span loading. In this way the bats can be divided into three groups: those weighing 6 to 8 g with a span loading of 0.29 to 0.35; those weighing 16 to 30 g with a span loading of 0.57 to 0.79, and those weighing 31 to 134 g with a span loading of 1.11 to 2.34. The buoyancy index is moderately high in all, being 3.29 to 5.05 while the aspect ratio is rather low, ranging from 2.51 to 4.10.

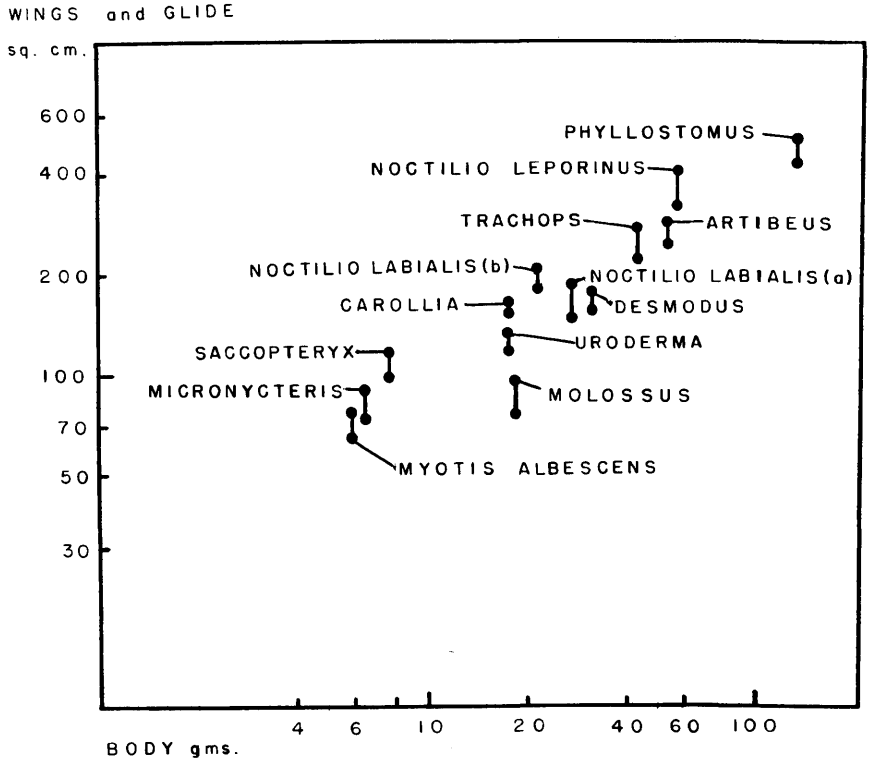

FIGURE 3. Plottings of areas for wings (low end of vertical lines) and glide (high end of vertical lines) (log scales).

DISCUSSION

In discussing these results a comparison with similar results on birds (Hartman, 1961) is of interest. The range of value is much smaller in bats, no doubt in part due to the small number of species (12) but not entirely so. The hearts are never as small relatively as in some ground birds (0.2 to 0.4 per cent in the tinamou and quail) nor as large as those in hummingbirds (2.0 to 2.5 per cent). A large heart may be able to sustain flight for longer periods than can a small heart if observations on birds hold true here (Hartman, 1961). This would indicate that bats remain in the air longer than do the quail and tinamou yet they may not have the endurance of the hummingbird. If the Bonda Mastiff Bat (*Molossus bondae*) has habits similar to *Eumops* sp., another member of the same family described by Vaughan (1959), its flight should be strong and fast and it could remain in the air for hours at a time. Its relatively large heart should be able to sustain such flight and with the low aspect ratio of its wings it would show great maneuverability and, if like *Eumops* sp., it could hover for several seconds.

Birds have a much greater range of ventral thoracic muscles than do bats, being 5.7 per cent in the grebe *Podilymbus* sp. and 33 per cent in the tinamou, *Tinamus* sp., and 36 per cent in the dove *Leptotila* sp. (Hartman, 1961). Birds likewise show a much greater range of activity in the air. The low for ventral thoracic muscles in our series for bats is 7.12 per cent while the high is 11.99 per cent.

The areas involved in maintaining the bat in the air are the wings, tail membrane, and body. The shape of the wings, their span, their aspect ratio and their camber are factors in aerial maneuvers whether in flight or gliding. These areas together with the flight muscles determine the buoyancy in air.

The relatively large wing areas account for the great maneuverability The lowest area, 3.40 cm^2/g is nothing like that found in some birds (e.g., 0.79 cm^2/g in ducks and 0.89 cm^2/g in tinamous). On the other hand, the 12.88 cm^2/g for bats is much higher than anything found in birds. (e.g., 8.6 cm^2/g). Poole (1936) showed that most bats have lower wing loading than do birds. A light wing loading enables bats to fly for long periods of time at slow speeds. Vaughan indicated that bat flight is less efficient than bird flight. The upstroke consumes relatively more power in bats than in birds because the wing surfaces in bats are continuous and do not allow passage of air as do the spaces between bird primaries. The wings of most bats is of high camber, making them efficient at low speeds. The uropatagium aids in braking as well as lifting.

The wing areas vary so much among different species that their flight habits must differ accordingly. A large wing can accomplish its task with a slower beat. Thus the Greater White-lined Bat (*Saccopteryx bilineata*), the Brazilian Small-eared Bat (*Micronycteris megalotis*), and the Paraguay Myotis (*Myotis albescens*) could produce lift with slower motion while the Spear-nosed Bat (*Phyllostomus hastatus*) would need to work more rapidly.

Vaughan pointed out that the bodies of most bats are more nearly flat than those of a majority of birds so that they are probably more effective as factors in lift during flight. He also says that the uropatagium acts much as the tail of birds since it moves up and down in synchrony with the wing strokes helping to keep the body on a fairly even keel. When the anterior part of the body is lifted by the wings this is counteracted through lifting of the posterior end of the body by the depressed uropatagium. This is the reason for including the uropatagium only in the glide area.

The buoyancy index (3.29 to 5.05) does not show quite as great a range in bats as that found in birds (2.70 to 5.86), but it is usually large. This index is, perhaps, the best measure of buoyancy since wing area varies as the square while body weight varies as the cube (George and Nair ,1952).

Likewise the aspect ration varies from 2.47 to 4.10 while in birds it ranges from 1.46 to 4.69 (Hartman, 1961). The moderately broad wings permit great maneuverability.

The two groups of Southern Bulldog Bats (*Noctilio labialis*) were thought to be different species when collected. However they were identified by Mr. George C. Goodwin of the American Museum of Natural History as the same. Both were adults collected along the Rio Chagres in January and February but in different years. Those in group "a" were definitely heavier than those in group "b". The heart percentage, ventral thoracic muscle percentage, and aspect ratios were the same but the wing areas and buoyancy indices differed considerably as has been pointed out. Perhaps they are different varieties.

This limited sampling of the great number of species of bats that exist may give a false idea of the range of flight equipment as compared with that in birds of which many more species (360) were studied (Hartman, 1961). However, as far as this report is concerned, there is much less variation in the flight equipment i.e., relative muscle size and relative supporting areas, than in birds.

Judging from a similar study in birds, bats should sustain flight fairly well and the buoyancy of their wings could permit considerable maneuverability. Indeed the flexibility of the wings in contrast to that of birds would permit quick change of direction or zigzag flight.

SUMMARY

Twelve species of bats distributed among six families have been studied.

Hearts range from 0.61 to 1.26 per cent of the body weight as compared with

0.20 to 2.50 per cent for bird hearts. Ventral thoracic muscles range from 7.12 to 11.99 per cent of the body weight compared with 5.70 to 36.00 per cent for these muscles in birds. Wing areas in bats run as low as 3.40 cm^2/g to as high as 12.88 cm^2/g, while in birds the range is 0.79 to 8.60 cm^2/g.

The buoyancy index is 3.29 to 5.05 for bats and 2.70 to 5.86 for birds. Similarly the aspect ratio of 2.47 to 4.10 is more limited than the indices of 1.46 to 4.69 for birds.

In general, it may be said that there is much less variation in flight equipment in bats than in birds. The mechanisms in bats should sustain flight very well and permit of greater maneuverability than similar mechanisms in birds.

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LITERATURE CITED

Hall, E. R., and **K. R. Kelson.** 1959. The mammals of North America. The Ronald Press Co., New York.

Hartman, F. A. 1961. Some locomotor mechanisms of birds. Smithsonian Misc. Collect. 143: 1–91.

George, J. C., and **K. K. Nair.** 1952. Wing spread and its significance in the flight of some common Indian birds. J. Univ. Bombay 20: 1–5.

Macalister, A. 1873. Myology of chiroptera. Phil. Trans. Royal Soc. 162: 126–171.

Poole, E. L. 1936. Relative wing ratios of bats and birds. J. Mammal. 17: 412–413.

Struhsaker, T. T. 1961. Morphological factors regulating flight in bats. J. Mammal. 42: 152–159.

Vaughan, T. A. 1959. Functional morphology of three bats: *Eumops, Myotis, Macrotus*. Univ. of Kansas Publications, Museum of Natural History 12: 1–153.